Ecological Theory and Community Restoration Ecology

Margaret A. Palmer[1,4]
Richard F. Ambrose[2]
N. LeRoy Poff[1,3,5]

Abstract

Community ecological theory may play an important role in the development of a science of restoration ecology. Not only will the practice of restoration benefit from an increased focus on theory, but basic research in community ecology will also benefit. We pose several major thematic questions that are relevant to restoration from the perspective of community ecological theory and, for each, identify specific areas that are in critical need of further research to advance the science of restoration ecology. We ask, what are appropriate restoration endpoints from a community ecology perspective? The problem of measuring restoration at the community level, particularly given the high amount of variability inherent in most natural communities, is not easy, and may require a focus on restoration of community function (e.g., trophic structure) rather than a focus on the restoration of particular species. We ask, what are the benefits and limitations of using species composition or biodiversity measures as endpoints in restoration ecology? Since reestablishing all native species may rarely be possible, research is needed on the relationship between species richness and community stability of restored sites and on functional redundancy among species in regional colonist "pools." Efforts targeted at restoring system function must take into account the role of individual species, particularly if some species play a disproportionate role in processing material or are strong interactors. We ask, is restoration of habitat a sufficient approach to reestablish species and function? Many untested assumptions concerning the relationship between physical habitat structure and restoration ecology are being made in practical restoration efforts. We need rigorous testing of these assumptions, particularly to determine how generally they apply to different taxa and habitats. We ask, to what extent can empirical and theoretical work on community succession and dispersal contribute to restoration ecology? We distinguish systems in which succession theory may be broadly applicable from those in which it is probably not. If community development is highly predictable, it may be feasible to manipulate natural succession processes to accelerate restoration. We close by stressing that the science of restoration ecology is so intertwined with basic ecological theory that practical restoration efforts should rely heavily on what is known from theoretical and empirical research on how communities develop and are structured over time.

[1]Department of Zoology, University of Maryland, College Park, MD 20742, U.S.A.

[2]Environmental Science and Engineering Program, Box 951772, University of California, Los Angeles, CA 90095-1772, U.S.A.

[3]Trout Unlimited, 1500 Wilson Blvd., Suite 310, Arlington, VA 22209, U.S.A.

[4]Corresponding author.

[5]Current address: Biology Department, Colorado State University, Fort Collins, CO 80523, U.S.A.

Introduction

The science of ecological restoration—that is, the development and testing of a body of theory for repairing damaged ecosystems—is in its infancy. Natural resources managers and regulatory agencies are wrestling with the development of prudent approaches for restoring damaged ecosystems; however, restorationists have received little input from the scientific community, even when efforts have been made to seek their advice. This is unfortunate, because judgments concerning ecological restoration and conservation are fundamentally based on conceptual or theoretical models of nature (Naveh 1994; Pickett & Parker 1994; Lubchenco 1995). On the flip side of the coin, research ecologists have generally not viewed restoration ecology as a field offering opportunities for advancing basic theory. Indeed, ecological restoration efforts may be ideal for testing important hypotheses in unique ways. For example, large-scale experimentation, including manipulations, may be more acceptable at restoration sites than in pristine settings. Further, interpretation of experimental outcomes may be easier because restoration sites often harbor simpler communities.

In this paper, we address the role of community ecological theory in restoration ecology. The practice of ecological restoration may benefit by an increased focus on how and when ecological theory can guide restoration efforts *and* a focus on how and when ecologists can use restoration settings to gain insight into how natural communities work. Further, the time is ripe for basic researchers to ask if current ecological theory is adequate

for the development of *principles of restoration ecology*. Where are the gaps in our knowledge? What new theory needs to be developed? What existing theory needs to be tested in a restoration context?

Community ecological theory is extremely relevant to restoration ecology because restoration efforts so often involve a focus on multi-species assemblages. Since these assemblages consist of populations of co-occurring species, they must be understood not only in terms of species interactions but also in terms of population processes, habitat and resource dynamics, and disturbance theory. There have been debates over whether or not communities can be described as units that are discrete, clearly defined, and integrative (i.e., defined by interactions). Without digressing into those debates, let us say that we agree with views similar to those expressed by Michael Palmer & Peter White (1994) in which they "liberate the definition of communities from particular space-time units" and conclude that community boundaries (and community theory) are somewhat arbitrarily set by ecologists in order to study operationally this level of ecological organization.

Clearly, communities exist in a landscape or sometimes a metapopulation context, and thus theories typically associated with ecosystem or population-level ecology (e.g., spatial ecology, source-sink population structure) are relevant to community ecology. However, *community ecology* does have something discrete to offer the field of *restoration ecology*. Thus we limit ourselves, in this essay, to a discussion of those theoretical areas that are typically associated with community ecology, freely recognizing that other theoretical areas (e.g., landscape ecology [Bell et al. 1997] or ecosystem ecology [Ehrenfeld & Toth 1997]) are relevant to understanding pattern and process at the community level.

Our essay is a discussion of those community-level topics we deem most relevant to restoration practices and theory. We address several major thematic questions, including: What are appropriate restoration endpoints from a community ecology perspective? What are the benefits and limitations of using species composition and biodiversity as an endpoint in restoration ecology? and, Can empirical and theoretical work on community succession "inform" restoration ecology? The problem of how to measure restoration at the community level is not trivial, particularly given the high amount of variability inherent in most natural communities. Community ecologists have long worked to make sense of this variability by developing theories for predicting ecological patterns and processes. Much of this theory is germane to restoration ecology and is the focus of this paper. Recent debates over the role of biodiversity in ecosystem stability, the functional role of species, and the role of habitat and natural disturbance regimes in maintaining communities have impli-

cations for how we approach ecological restoration. Finally, successional processes in the broadest sense, including the roles of dispersal, colonization, and community assembly theory, are central to restoration. Throughout, we highlight specific questions that are critically in need of further research to advance the science of restoration ecology.

Choosing Appropriate Restoration Endpoints

Defining ecological restoration is not as obvious as it appears at first glance. The Society for Ecological Restoration has reevaluated and altered its definition of restoration ecology at least five times in the last six years. Further, there continues to be much debate over how we assess restoration, including what constitutes a reference or comparison site and what metrics are most appropriate to assess restoration (Michener 1997; White & Walker 1997). The National Research Council's (1992) definition of restoration as "returning a system to a close approximation of its condition prior to disturbance, with both the structure and function of the system recreated" implies that we know what should be measured to assess restoration, i.e., we know the appropriate endpoints.

What we select as endpoints may determine our evaluation of restoration success, particularly since the units of resolution (e.g., presence/absence of a species vs. absolute abundances) may constrain assessment. From a community ecology perspective, appropriate *structural endpoints* include measuring species richness of focal groups (Davis 1996) or entire assemblages. *Functional restoration endpoints* in the strictest sense refer to measures of processes such as primary or secondary production. Restoration of a system to its proper functional state may require restoration of key linkages related to food web structure (e.g., number of trophic levels and their connectance) or of taxa critical to material processing (e.g., functional groups necessary for processes critical to particular systems, such as decomposers in detrital-based systems). There is considerable evidence that a feedback exists between species composition and ecosystem processes and that many ecosystem processes will develop over different time scales. This means that restoration in practice may involve the setting of sequential, multi-step goals: restore desired species richness (community *structure*) → monitor the development of community structure → verify that linkages between community structure and *function* have been established.

Imbedded in many definitions of ecological restoration is the notion that a restored community is stable, i.e., persistent over time. Restoration in practice often takes this to the extreme by assuming that ecological stability is synonymous with stasis. For example, the goal of many stream restoration projects is to attain

geomorphic stasis (Rosgen 1994; Smith & Prestegaard 1995). This concept is flawed because it fails to recognize that the very nature of stream channels is to move, and physical stasis in no way ensures ecological "stability." Indeed, equilibrium concepts are no longer broadly accepted by ecologists as adequate for understanding community structure. Many communities exist in perpetual states of nonequilibrium or dynamic equilibria where natural disturbance prevents most populations from reaching maximum densities (Wiens 1984; DeAngelis & Waterhouse 1987; Pickett et al. 1992). Natural variability both physically and biologically is part of nature (Duarte 1991; Li & Reynolds 1994; Horne & Schnieder 1995; Palmer & Poff 1997) and the challenge to restorationists is to develop tools for assessing acceptable levels of variability in restored systems (White & Walker 1997). Perhaps the way to proceed is to view local communities in regional contexts (Menge & Olson 1990; Cornell & Lawton 1992; Ricklefs & Schluter 1993) or historical contexts (Richter 1995) that act to define the local restoration *potential.* Regional constraints, such as limits on the pool of species available to colonize damaged sites or limits set by regional climate, may determine which species we can *potentially* expect in restoration sites. However, actual species establishment in restored sites depends ultimately on local habitat constraints, *both* abiotic (e.g., substrate types) and biotic (e.g., species interactions).

Future research questions

- How much variation in community attributes is acceptable in restored systems?
- How do we quantify natural variability in community-level properties (e.g., trophic structure) given often limited reference or pre-impact data?
- How do we define the restoration potential for community attributes (i.e., identify regional contexts)?
- To what extent can we practice hard versus soft engineering restoration practices (Gore et al. 1995) that allow systems to be dynamic?

Biodiversity and Restoration Ecology

Central to community ecology is the study of species diversity, particularly the creation and maintenance of local and regional biodiversity. Of all areas in community ecology, the study of species diversity probably has the longest history and the most voluminous literature. Even a cursory look at recent publications reveals an abundance of new books and articles on biodiversity (e.g., Ricklefs & Schluter 1993; Huston 1994; Humphries et al. 1995; NRC 1995). It is generally well accepted that restoring biodiversity is desirable for a variety of ecological, applied, and aesthetic reasons. Restoration projects are,

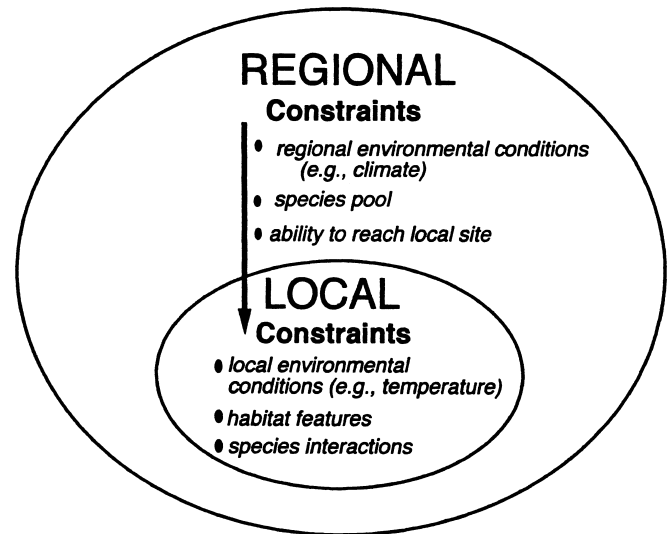**Community Restoration = *f* (regional + local constraints)**

Figure 1. Successful restoration of a community depends on both regional and local factors. There must be an intact supply of colonists at the regional scale that can survive the environmental regime and reach (disperse to) local sites. For species to become established locally, there must be suitable local conditions, including environmental and habitat features (e.g., abiotic factors, habitat structures, and natural disturbance regimes such as flooding or fires). Finally, species interactions may preclude species establishment locally.

in effect, experiments that introduce different numbers and kinds of species, experiments that can be used to test the effects of species richness and species roles on community recovery and functioning. The effort expended in trying to restore a community can range from minimal to extremely extensive, with concomitant costs. Therefore, restorationists have to be concerned with cost/benefit ratios. It is important to determine the minimum numbers and types of species necessary for proper community functioning.

Can community or ecosystem stability be increased by adding more species (enhancing diversity) or particular species in the restoration process? If the answer to this is yes, it implies that restoration success may depend on careful consideration of community level attributes, not just a focus on single species or clusters of "desirable" (e.g., endangered) species. May (1973) presented mathematical evidence that diverse systems are less stable than simpler ones. The idea was that the more diverse a community, the more complex the web of species interactions and thus the larger the effect disturbances would have on the system. We now know (and actually, May suggested this himself just one year after his 1973 paper) that diversity may make individual species more vulnerable to extinction, but total community or ecosystem properties (e.g., energy transfor-

mation, biomass) may be stabilized, since some species compensate functionally for others (Naeem et al. 1994; Tilman et al. 1994; Tilman 1996).

This suggests that some communities or ecosystems may be more stable if you increase diversity, but individual species may or may not be persistent. Thus, a clearly defined restoration goal is imperative at the outset of each project. For example, if the goals are related to management of endangered species, then a restorationist's concern with biodiversity need not be to maximize the number of species but simply to understand how biodiversity influences the establishment and persistence of the focal species. This is not necessarily simple, since it may require an understanding of complex species interactions—both direct and indirect effects— and the context in which the interactions occur (Karieva 1994; McPeek 1996). If the goal is to restore a community to a proper functional state, then restorationists may care little about individual species and focus instead on restoring functional groups or suites of species, as outlined in the next section.

Future research questions

- Do we have existing data to explore the relationship between community or ecosystem stability (e.g., of a restored site) and species diversity? If so, for which systems?
- What is the relationship between restoration of community structure (e.g., species composition) and restoration of function (e.g., material processing)?

Restoration of Function: Do Species Matter?

Proper ecological "functioning" is a loose concept but basically refers to keeping systems "working," i.e., cycling energy and nutrients through trophic levels to retain system integrity (Schulze & Mooney 1993; Davis & Richardson 1995). Thus, a system that is properly functioning is one that will persist despite natural environmental fluctuations. So, for example, if decomposers are essential to the integrity of a community's food web, then perhaps we should focus first on restoring the amount and tempo of organic matter inputs to the system and second on the introduction of suites of decomposing species.

When focusing on system function, we need not concern ourselves with individual species *if* there is some degree of functional redundancy among the pool of colonists. With high functional redundancy, the relationship between biodiversity and ecosystem function (and stability) may plateau (Tilman et al. 1994). This suggests that it may be possible to set a minimum for restoration of species richness that ensures proper functioning. This clearly relates to the initial conditions: how much

of the community needs to be established initially in order for the site to ultimately support the desired community, with its proper structure and function?

The idea that there may be thresholds of species diversity needed to ensure recovery of function is somewhat controversial because some scientists argue that all species matter and that assuming some species are more important than others in communities is poorly substantiated in general (Hay 1994; Gitay et al. 1996). In restoration efforts, we believe there is a greater need for pragmatism and acceptance that restoration of all species will not typically be possible. Unfortunately, at this time there are few data on functional redundancy and the role of species in system functions. The sparse data available apply to only a few terrestrial or soil ecosystems (e.g., Lawton & Brown 1993; Freckman 1994; Tilman 1996). Work on this topic for aquatic systems is rare (Covich 1996), and, in fact, aquatic systems were recently targeted by the Scientific Committee on Problems of the Environment as being in dire need of an understanding of how species affect system processes (SCOPE 1996).

Efforts targeted at restoring system function must not ignore the possibility that some species play a disproportionate role in communities. The concept of the keystone species is quite old and focused most often on the fact that some species may be strong interactors having large impacts on community structure (e.g., Paine 1996). More recently there has been a push to rethink our concept of keystone species based on whether or not a species has a disproportionate effect on an ecosystem relative to its biomass contribution. Such a species is said to be a keystone species, or engineer (Jones et al. 1994; Brown 1995; Stone 1995). This is a broad concept in which "effect" can include the creation, modification, or maintenance of habitat (Jones & Lawton 1995). In restoration practices, we should think carefully about the needs of such species, since their successful reestablishment may determine community restoration outcome and maintenance of diversity or function once reestablished.

The difficulty is that keystone species are not always easy to identify. This is particularly problematic if a keystone species is not abundant or its actions are not obvious. Boyer and Zedler (1996) found that an inconspicuous beetle controlled scale insects that damaged cordgrass; when the beetles were absent from the constructed marsh, cordgrass performance was poor. Specific studies or field experiments are often needed to identify and confirm the role of keystone species.

Non-native species may also have huge impacts on communities. Exotic species may alter species diversity or prevent the reestablishment of native species in restoration sites (Simberloff 1990; Vitousek 1990). Human disturbance often increases the likelihood of invasion by exotics (Holzner et al. 1983; Mills et al. 1994). Once

established, these species may be particularly difficult to remove, since they are often subject to less pressure from competition or predation than are native species. It may be necessary, or at least more practical, to re-think restoration practices that do not require the exclusion of exotics that have become well-established. If, on the other hand, these exotics preclude any reasonable level of restoration, then we must develop effective ways to reduce their impact on a system.

Future research questions

- Is the existing evidence of functional redundancy sufficient to allow different subsets of a regional species pool to be selected for restoration efforts? If so, for which systems?
- In which systems is the presence of keystone species required for successful restoration?
- How do we assess the degree to which established exotic species will prevent successful restoration of a functioning community?

Is Restoration of Habitat Sufficient?

While the study of what fosters the establishment and maintenance of diverse communities is far from complete, there are some broad generalizations that most ecologists would accept. One of these is that as habitat heterogeneity increases, generally so does biological diversity (MacArthur 1965; NRC 1992). Indeed, central to many restoration efforts is the assumption that rehabilitation of physical habitat diversity will lead to the restoration of biological communities. Obviously, practitioners have to begin somewhere, and given that environmental heterogeneity is associated with increased species diversity in many terrestrial and aquatic habitats (Giller et al. 1994; Huston 1994), we generally endorse rehabilitation of habitat heterogeneity in restoration efforts. However, it is important to recognize that the assumed relationship between habitat heterogeneity and biodiversity *in a restoration context* remains largely untested.

The importance of habitat structure in restoration can be stated as the Field of Dreams hypothesis: "if you build it, they will come." There is some support for this hypothesis. In wetland restoration, "getting the hydrology right" seems to be the most important ingredient for restoration success, with proper soil characteristics also necessary. Although wetland restoration projects generally include vegetation planting as well, there is some thought that the proper vegetation will colonize as long as the physical conditions are there. However, this has not been demonstrated, and the habitats and conditions under which this would occur are not known. At the other extreme, the initial floristics model of succession proposes that all species desired on a site

must be reintroduced for successful restoration, because few will be able to colonize. Research is needed to determine which model is more accurate for different communities and different conditions. Almost invariably, the Field of Dreams hypothesis is invoked with respect to wetland fauna, since animals are rarely introduced or manipulated in wetland restoration projects. Unfortunately, this hypothesis is generally assumed rather than tested. It needs to be rigorously tested in communities where it has regularly been invoked, and its generalizability to different habitats and different taxa also needs to be tested.

We also need to know much more about the role that spatial habitat *arrangement* plays in the success or failure of restoration efforts. It is now clearly established that the shape and size of a habitat may determine the number of species and other community attributes (Forman 1995). For example, a greater fraction of "edge" versus "interior" species is expected in habitats with large perimeter/area ratios (Galli et al. 1976; Helle & Muona 1985). Additionally, the inclusion of critical habitat (e.g., for reproducing or surviving natural disturbance) may be essential for long-term persistence of communities. All habitat patches are not equal, and the ability to move freely between patches that vary in resource quality and quantity may be essential for many species (Hanski 1995), particularly if some patches serve as refugia (Sedell et al. 1990).

Future research questions

- Are there critical thresholds of physical habitat restoration that will ensure restoration of species and ecological function?
- At what spatial scale do we need to restore species diversity and how does this relate to successful restoration of ecosystem function?
- Are there key spatial attributes (e.g., connectivity between habitat patches that allow adequate dispersal) that are required for species persistence?

Restoration and Natural Disturbance Regimes

It is generally agreed that some low level of *natural* disturbance (e.g., fires, floods) may enhance biological diversity. Whether one embraces Connell's (1978) intermediate disturbance hypothesis or more complex explanations of the relationship between disturbance and species diversity (Huston 1979, 1994), the implication is that restoration of natural disturbance regimes must be a part of rehabilitation efforts. As a consequence of the important role of disturbances, restoration cannot simply reintroduce species, but must also consider small- and large-scale disturbances and how these influence the sustainability of a restored commu-

nity. This may be one of the greatest challenges of restoration, both because the nature and role of disturbance are not always obvious, and because reproducing the essential dimensions of the disturbance may be difficult. The need for continued manipulation (either active or as the result of processes that have been established) after initial establishment of species on the restoration site requires that we identify the dimensions of disturbance regimes that are essential for successful restoration.

By dimensions of disturbance, we mean the size, intensity, duration, seasonality, etc. of a disturbance. Note that both spatial and temporal aspects are important. For example, Moloney and Levin (1996) showed that the impact of disturbance depends on a complex interaction between the life history characteristics of the species making up a serpentine grassland community and the spatial and temporal structure of the disturbance regime. This issue has two components. First, the dimensions of disturbance in the natural community must be identified. This can be a difficult task, both because of the complexity of the disturbance regime and because of the lack of an appropriate reference site. Second, after the disturbance regime has been identified, its essential elements must be defined. It may not be necessary to duplicate exactly the natural disturbance. The disturbance regime in tallgrass prairie provides an example of both aspects. It appears that the disturbance regime includes at least two components, fire and grazing, which interact in a complex way (Vinton et al. 1993). Unfortunately, there is no remaining "natural" prairie habitat where the natural disturbance regime occurs, so identifying the exact nature of the disturbance is not simple. With respect to grazing disturbance, it may not be necessary to have large herds of free-roaming bison; instead, grazing by cattle under a specific regime might provide the essential element of that disturbance.

If one cannot reestablish the intensity or frequency of past disturbance regimes, it may be possible to factor into restoration designs periodic disturbances that mimic natural events. River regulation in the Grand Canyon has resulted in loss of high flows that create and maintain important sandbar habitat for native species. The experimental release of water from the Colorado River storage system in the spring of 1996 was an attempt (largely successful) to mimic pre-dam flooding to redistribute sand and recreate sandbar habitat in the canyon (Schmidt 1996). Even if this is done only on a decadal scale (certainly not the temporal scale that existed pre–flow regulation), it may play a key role in system restoration.

Future research questions

- What is the evidence that natural disturbance enhances restoration?

- How do we restore a "natural disturbance regime," especially if the signal is changing over time or significant landscape alterations (e.g., from forest to agricultural lands) have occurred?
- What is the minimum level of manipulation required to mimic natural disturbance events?

The Roles of Succession and Dispersal in Restoration

In the classic sense, ecological succession is viewed as a progressive change in community composition and dynamics over time (Putnam 1994). From a restorationist's perspective, it would be ideal to work on systems that are typified by predictable directional changes in structure during community development. In such a system, we could view any attempt to restore an altered community as an attempt to manipulate natural successional processes. Such manipulations might attempt to accelerate natural succession, so that the community develops along the same lines as it would in the absence of intervention, but the desired endpoint is reached sooner. Manipulations might also attempt to bypass some of the stages of natural succession, for example by establishing some late successional species in the initial plantings. In such cases, the goal is to accelerate the rate of natural succession so we achieve the desired community sooner rather than later.

The classic Clementsian view of succession as a deterministic process with the community moving toward a climax condition after passing through a series of distinct seral stages is not universally applicable (Connell & Slatyer 1977). Disturbances and stochastic events can introduce substantial unpredictability to community patterns over time (Fisher 1983; Levin 1989; Roughgarden 1989). The whole field of supply-side ecology, with an emphasis on recruitment limitation and stochastic arrival of colonists, suggests that in many systems the succession "paradigm" may not apply (Roughgarden et al. 1987; Olafsson et al. 1994). Much of the supply-side literature has focused on when and if variation in settlement rate controls population structure, emphasizing that colonization may be more important than internal population processes such as predation and competition (Niering & Goodwin 1974; Underwood & Fairweather 1989; Palmer et al. 1996).

Given that both deterministic and stochastic processes may be important in community development, what are the implications for restoration ecology? If succession theory allows one to predict the trajectory of communities, then it may be a powerful tool for restorationists, for example, to control the direction by timed seeding programs. This is most likely to be useful in systems that have strong species interactions and infrequent or highly predictable disturbances, so that local interactions largely govern community development

(Cornell & Lawton 1992). In such systems, community assembly theory suggests there may be "rules" that constrain membership in a community (Drake 1991; Wilson 1995; Wilson & Whittaker 1995), and these rules may have important implications for how restoration should be approached. Careful attention should be given to the order in which species are introduced in such systems so that priority effects and direct species interactions do not interfere with the desired restoration sequence.

The importance of initial conditions is not restricted to which species are first established at a restoration site. Physical conditions, including hydrology, soil characteristics, topography, and so on, can be critical (Bentham et al. 1992). For example, inappropriate sediment characteristics (low nitrogen and organic content, coarse grain size) can affect wetland community development (Langis et al. 1991; Moy & Levin 1991; Gibson et al. 1994). Although we recognize that initial conditions can affect restoration outcomes, we generally do not understand much about the nature of these effects.

In less biologically predictable systems that have larger stochastic elements to recruitment, community "assembly" may be a function of dynamic dispersal processes and less predictable local interactions among species post-recruitment (Sale 1977). In such a situation, guild-based views of community assembly (Keddy 1992; Fox & Brown 1995) may be more appropriate, so that the restorationist is more concerned with environmental and biotic interaction effects on suites of species with particular functional traits.

Regardless of what happens once colonists arrive, restorationists must worry about the scale of restoration and the connectedness of the site to a regional colonist pool, unless seeding is tractable and affordable. Indeed, the distance to the nearest intact regional pool of colonists in conjunction with the degree of site degradation will determine whether or not species must be manually introduced to a restoration site and the extent of site preparation needed prior to their introduction (Cairns 1993).

With respect to the regional pool of colonists, theoretical and empirical work suggests that restoration efforts will fail if we do not evaluate the need for dispersal corridors (Forman 1995), if we do not meet critical threshold connectivity (between restoration site and regional pool) levels (Hansson et al. 1995; With & Crist 1995), or if the arrangement of physical habitat structure critical to species persistence is not ensured (Harrison & Fahrig 1995). These are particularly important for the restoration of communities that rely on the continual flux of individuals to and from regional dispersal pools (Holt 1993; Palmer et al. 1996). Indeed, because local processes such as competition and predation may be strongly influenced by regional dispersal, community

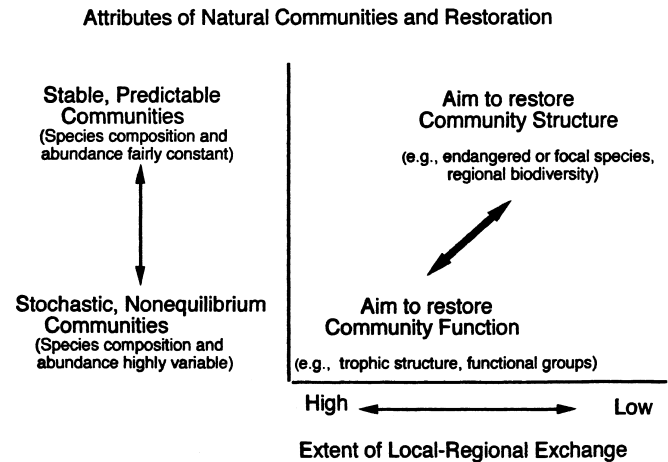**Attributes of Natural Communities and Restoration**

Figure 2. The utility of different community ecology theories in restoration efforts will vary depending on attributes of the natural (unperturbed) communities. For those that have fairly predictable community structure through time (species composition and abundance relatively constant), a focus on the restoration of community *structure* (e.g., particular species) may be possible. In such cases, community assembly theory and ecological succession models may be useful for deciding the order of species introduction and for deciding when the level of restoration is sufficient to allow natural communities processes to take over (i.e., the site is far enough along successionally to be self-sustaining). For those communities that exhibit stochastic flux in species composition and abundance, a focus on restoration of community *function* (e.g., community processes like decomposition) may be more appropriate. In such cases, supply-side ecology, lottery models, or recruitment limitation theory may be useful in deciding how much connectivity to regional dispersal pools is required and what level of variance in community structure is reasonable for restored sites.

assembly at restored sites may be a function of the influx and efflux of individuals in some systems (Gaines & Bertness 1993).

The spatial pattern of interventions (e.g., planting patterns and distribution of structural elements) is also likely to influence the course of community development. For example, different planting patterns in a mine reclamation project in Wyoming led to different spatial and age-structure patterns of vegetation and different soil characteristics and biota (Parmenter & MacMahon 1983). This result was obtained because the plantings were done in a careful experimental design; however, experimental manipulation of spatial patterning of interventions is rarely done. The temporal patterns of interventions are also likely to influence the course of community development. Community development may differ depending on when organisms at specific life stages are introduced. For example, community development may proceed along one trajectory if initial plant establishment is from seed germination

and another trajectory if sod blocks with intact soil biota are transplanted. Sequencing of interventions is also likely to be important. Community development may depend on when different stages of site preparation take place, where in the sequence planting occurs, and so forth. In the prairie example, there might be different outcomes if grazing follows rather than precedes burning.

Future research questions

- Do we have an adequate knowledge of the roles that colonization source, rates of movement, and the sequence of species introductions play in community restoration success?
- Can we identify communities in which it is possible to "manipulate" natural successional processes to accelerate restoration?
- Can we predict how much site preparation and transport of species into an area are needed as a function of the extent of local and regional degradation?
- Is community assembly theory useful for restoration in practice?

Closing Comments

One of our goals in writing this paper was to stress that the science of restoration ecology is so intertwined with basic ecological theory that practical restoration efforts should rely heavily on what is known from theoretical and empirical research on how communities develop and are structured over time. Great care should be taken in selecting restoration endpoints so that the goal guides project implementation and assessment. When the goal is to reestablish a functional community, one should focus on the rehabilitation of functional groups or clusters of focal species, not the needs of single endangered species. Even when the goal is aimed at a particular species, efforts must include broad perspectives since the reestablishment and persistence of that species depends on the regional environmental context (the ability of the system to supply recruits and support established individuals) and on species interactions once the community is established. The need to focus on dispersal and colonization dynamics is particularly important since many of our project sites are highly degraded *and* disjunct from a healthy regional pool of colonists. Community theory can guide seeding processes (e.g., seeding processes based on known patterns of community structure; Howe 1994).

We can identify some areas of community theory so poorly understood that our ability to restore damaged ecosystems may be greatly hampered. Research in these areas will benefit both basic ecology and restoration practices. We will point out just two of these to serve as examples. First, the relationship between dispersal/col-

onization dynamics and habitat arrangement, particularly in the face of natural and human-induced disturbances, is poorly understood for most systems. Spatial ecology, patch dynamics, and metapopulation theory are but a few examples of basic research areas that we need much more work on—particularly in a restoration context. Second, links between community or ecosystem function and biodiversity are not established for most species. If we can learn which species really matter to system functioning, not only will we have a much better understanding of the relationship between structure and function in natural systems but we may be able to target particular species or functional groups in order to restore a system to a self-sustaining level of functioning. In sum, we expect that the use of community ecological theory by restorationists will contribute not only to the development of a science of restoration ecology but to basic ecological research.

Acknowledgments

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